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Parrot ecology in a modified landscape, Tambopata, Peru.

Peter Cowen

Student Number: 04249591

Submitted by Peter Cowen, in part fulfilment of the Master of Science degree in Conservation Biology, awarded by Manchester Metropolitan University, through the Division of Biology in the School of Biology, Chemistry and Health Sciences.

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Abstract

Parrots are known to be frugivores but also exploit many other food items that the forest provides. As more pristine rainforest is deforested, modified landscapes may be important for parrot communities. In this study I assessed the abundance of parrot species in secondary forest at two sites in Tambopata, Peru, and documented important food resources for the parrot community as a whole and for individual species. Variable line transects were performed in primary and secondary forest in order to calculate density estimates using DISTANCE. This was then related to foraging observations which were recorded during census walks and opportunistic events. Habitat variables were also recorded in order to study habitat associations and were analysed using Principal Component Analysis. The parrot community in secondary forest was dominated by smaller bodied parrot species (e.g. Cobalt-winged parakeets *Brotogeris cyanoptera* and Black-capped parakeets *Pyrrhura rupicola*) whereas larger bodied parrots (e.g. Scarlet macaws *Ara macao* and Mealy parrots *Amazona farinosa*) were associated with primary forest. Parrots (mainly parakeets and *A. severa*) heavily consumed flowers of *Ochroma pyramidale* and *Cecropia peltata* and may be potential tree pollinators. The data presented here indicate that secondary forest holds important, albeit seasonally available, food resources and attracts a significant parrot population. Although, high levels of density estimates and foraging events may be linked to seasonality. Therefore, future conservation practices should not just include pristine forest but also modified secondary forest.

1. Introduction

Psittacines (Parrots) are a diverse order of birds (>330spp) which occur primarily in Australia, the Neotropics, Africa and Asia (Forshaw 1989). They inhabit a wide range of habitats from dry semi-open country to tall rainforests (Forshaw 1989). Neotropical parrots live in many settings and have evolved to become very ecologically flexible. New World parrot diversity is highest in the western Amazon Basin where communities commonly include more than 15 species. This diversity peaks in south-eastern Peru with various sites reporting 18 to 20 species (Terborgh 1986) including the endangered Blue-headed macaw *Primolius couloni* (Tobias 2007) and the critically threatened Amazonian parrotlet *Nannopsittaca dachilleae* which was only discovered in 1985 (O'neill *et al.* 1991).

Approximately one third of parrots are threatened with extinction, and due to anthropogenic changes many species have become locally or regionally extinct (Collar 1997). As with many large vertebrates, parrots are adversely affected by these anthropogenic activities which can take the form of road creation, human settlements and habitat degradation. In Latin America alone, 46 species are thought to be at risk of global extinction (Snyder *et al.* 2000). Species such as the Spix macaw *Cyanopsitta spixii* have already become extinct in the wild due to high levels of persecution (Juniper 1990) and populations of the Great green macaw *Ara ambigua* are rapidly declining (Berg 2007).

In spite of their importance in the forest bird canopy community and their potential influence on forest diversity, the natural history of parrots is poorly known with little information on over 75% of recognised species (Collar 1998). Information on diets is vital for understanding species niches, community roles and potential impacts on other species (Moegenburg 2003). This lack of information hampers important conservation measures such as reserve planning. Apart from island species, parrots are notoriously difficult to census which has left them largely unstudied (Terborgh *et al.* 1990).

Many species forage over large tracts of forest habitat ranging from dry to wet areas (Ragusa-Netto 2005). While they may be both habitat and foraging specialists, most species are generalist, often exhibiting seasonal dietary shifts (Galetti 1993; Ragusa-Netto 2006; Ragusa-Netto 2007). Individual species are able to exploit a wide variety of food resources from flowers and nectar (Ragusa-Netto 2007), to insect larvae in galls (Renton 2006) and seeds of different plant species (Forshaw 1989). Feeding on seeds makes them an important and effective pre-dispersal seed predator but this has rarely been documented (Matuzak *et al.* 2008). Recently, some parrot species have been identified as potential pollinators but again, few studies are available to support this (Ragusa-Netto 2004; Ragusa-Netto 2006; Ragusa-Netto 2007).

Few plant species fruit and flower year round so diets of birds may change as abundance and availability of food sources vary in both time and space (Wiens 1981). These annual variations in food supply have important implications for parrot life history patterns (Brightsmith 2006). Food abundance shifts can force changes to different food sources or displacement to more favourable areas (Terborgh 1986; Ragusa-Netto 2005). This dependence on selective food sources can make wild populations vulnerable to changes in supply (Matuzak *et al.* 2008).

Habitat loss and fragmentation is one of the main causes of the decline in tropical rainforest biodiversity and often creates a mosaic of modified rainforest. Modified forest is characterised by smaller trees and a decrease in species diversity (Scales *et al.* 2008) Vegetation is markedly different as high levels of light penetrating through the canopy supports an increase in growth of dense ground vegetation and fast growing pioneer trees. As pristine forest becomes increasingly fragmented and secondary growth increases, it may be important to conserve these habitats if they hold significant food plant resources.

A two month study was conducted between the months of June and August 2008 with the aim of studying the importance of a modified landscape to a rich parrot assemblage in Tambopata, southeast Peru. Two sites were chosen, the first Refugio Amazonas which is situated in primarily pristine forest; the second, Inotowa which is located approximately 14km away from the first site. Both sites are found along the Rio Tambopata. The objectives were to:

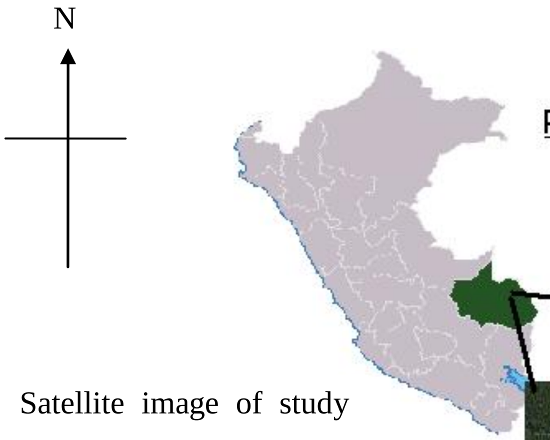
1. document plant species and plant parts consumed in secondary forest by parrot species.
2. determine key food resources.
3. calculate density estimates for both primary and secondary forest.
4. determine differences between primary and secondary forest that may account for differences in observed parrot communities.

2. Methods

2.1 Study Site

Data collection took place between June 11th and August 7th 2008. The study was located in south-eastern Peru, in the Tambopata province of the Madre de Dios department which is part of the Endemic Bird Area 068 (EBA) (Stattersfield *et al.* 1998). The area is situated in the Tambopata National Reserve (TNR) (274 690ha) created in 2000, formerly part of the Tambopata Candamo Reserve Zone (TCRZ) (1.5million hectare) until it was split into the TNR and Bahuaja Sonene National Park (BSNP) with the latter established in 1996 (537 053ha) (Gonzalez 2000). Average annual temperature is 26°C, ranging from 10-38° with annual precipitation of 1600-2400mm. The dry season occurs from April – October in which rainfall is limited to 90 – 250mm (Brightsmith 2004).

Two field sites were chosen (Fig. 1): Site one (12°52’43.05”S 69°24’39.87”W) situated at Refugio Amazonas lodge located in the TNR. Site two (12°48’32.33”S 69°18’09.91”W) is sited in the vicinity of Inotowa Lodge which is in the buffer zone



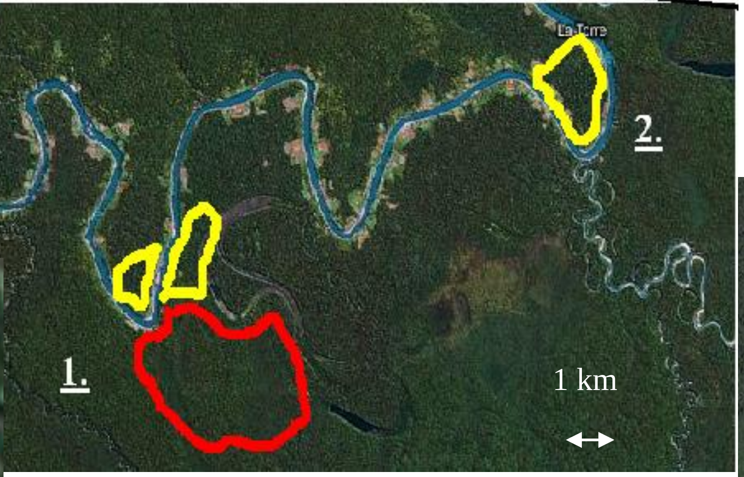


Figure 1: Satellite image of study sites. Red = transects in primary forest, yellow = transects in secondary forest. Numbers represent site.

Figure 2: Satellite image of study site 1. Transects: El Peter (1) and Chacra (2).

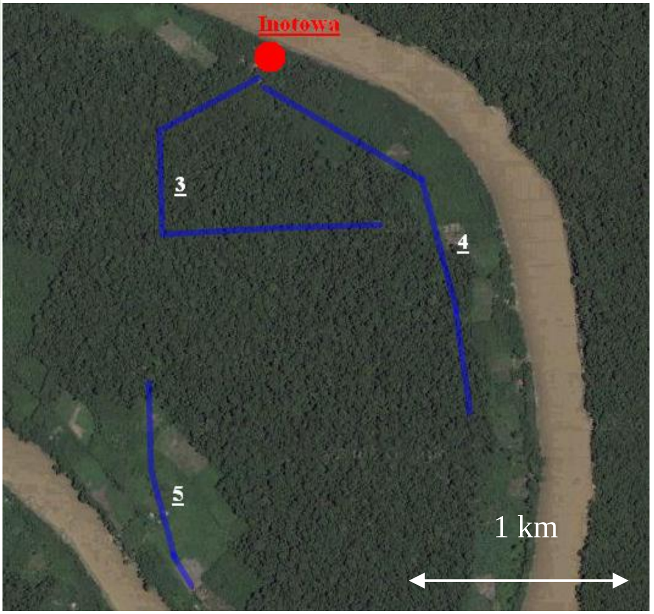


Figure 3: Satellite image of study site 2. Transects: Shuchupe (3), Maximo (4), and Community (5).

of the reserve. A total of 7 km of transects were available in secondary forest and 8km in primary forest (Table 1). At site 1 there were two transects in secondary forest both 1km in length and four transects located in primary forest (Fig. 2). Site 2 contained a total of 5 km split between three transects in secondary forest (Fig. 3). In all areas sampled, transects were set up along existing paths of widths approximately 2 m established for ongoing research in the area. One new transect ‘El Peter’ was established in the direction of a fixed bearing, avoiding natural obstacles e.g. lakes and rivers. Census walks were undertaken until at least 10 repetitions occurred for each transect. All transects were marked with tape at intervals of 50 / 100 m to aid distance measurements.

Table 1: List of transects for both forest types at each study site.

Transect	Habitat Type	Length (Km)	Map Code
El Peter	Secondary	1.0	1
Chacra	Secondary	1.0	2
Shuchupe	Secondary	2.0	3
Maximo	Secondary	2.0	4
Community	Secondary	1.0	5
Subtotal	-	7.0	-
ARA	Primary	2.0	6
El Gato	Primary	2.0	6
Condenando	Primary	2.0	6
Castana	Primary	2.0	6
Subtotal	-	8.0	-
Total	**-**	**15.0**	**-**

2.2 Bird Census Methods

Variable distance line transects were conducted following recommendations from Buckland *et al*. (2001). Transects were walked at an average speed of 1 km / h and took between one and three hours to complete, depending on transect length. To avoid bias, censuses were walked in rotation and between three time periods: 06:00-08:00, 08:00-10:00 and 15:30-17:30 corresponding to times of peak parrot activity.

DISTANCE (Lakke *et al.* 2006) was used to calculate density estimates for all parrot species for both primary and secondary forest. The observer recorded all parrots seen or heard, the number in the group when seen, and the perpendicular distance to the geometric centre of each group of perched birds (Lloyd 2004). Individual species density estimates were calculated when there were over 20 encounters, as lower counts would not produce a reliable estimate (Buckland *et al.* 2001). Records of parrots in flight were excluded from the analysis as aerial records clearly violate key assumptions of distance sampling (Marsden 1999; Evans *et al.* 2005). Records were entered in clusters, and density estimates were based on mean group size (Buckland *et al.* 2001). Model selection and fit were assessed using Akaike Information Criteria (AIC) minimization criterion and goodness-of-fit tests (Buckland *et al.* 2001). To test for significant differences estimates were compared using Z tests.

Diet was determined by observations of feeding activity; estimates of important food plant resources are based on the frequency of feeding bouts on said species (Snyder et al 1987). During the census walks detection of foraging birds was by direct observations, vocalisations or by falling fruits. When feeding parrots were encountered the following were recorded: date, time, location, species (irrespective of time spent foraging and amount of food ingested), number of birds and the plant part eaten i.e. fruit, pulp, seed or flower. Opportunistic events of foraging activity were also recorded e.g. when foraging walks were not taking place. An observation of one or more birds feeding was recorded as a single feeding bout. However, if a single bird or group flew and fed upon another plant of the same or different species an additional feeding bout was recorded (Galetti 1993; Renton 2001).

Identification of plant species was performed in the field whenever possible, while further identifications were performed from photos by staff of the University of Cusco field museum. Diet observations were analysed using the number of individuals observed feeding on a particular resource. Niche breadth was evaluated using Standardised Levin's Index (Levins 1968). Values close to 0 indicate dietary specialisation and values close to 1 indicate a broad diet (Colwell *et al.* 1971). Chi-squared tests were used to examine differences in foraging events between habitats.

2.3 Habitat Sampling Methods

Habitat surveys were conducted along the foraging trails at both sites, modified from Jones *et al*. (1995) and Marsden *et al*. (1999). A brief summary of the methods is as follows: At each census point (every 100 m) along the transect, the nearest five trees with a diameter at breast height (DBH) larger than 0.2 m located in a 20 m radius around the point were selected. The DBH, distance to the census point and the height of each tree (calculated with the aid of a clinometer) was recorded. The presence or absence of fruits and flowers was noted for each of the five trees. At each plot the percentage cover of vegetation at canopy level was estimated and given one of the following values: 0%, 25%, 50%, 75% and 100%. While this estimate may not reflect the absolute percentage of vegetation, they should still be broadly comparable as estimates were made by the same recorder.

As an indication of the sites recent history the tree 'architecture' was recorded using methods suggested by Jones *et al*. (1995). It was noted whether the site of first major branching was above or below half the tree's height. The presence of large scars on the trunk and in which direction the branches grow was also noted. Generally, 'primary forest' trees have branches above half its height whereas those branching below half its height have grown up in 'secondary forest'. Trees growing around a tree fall or in secondary forest that is maturing may shed their branches to form scars so they are able to push up to reach the canopy (Jones *et al.* 1995). Alternatively, the lower branches may grow vertically in order to push the crown into the canopy. Both of these reactions are said to be symptomatic of regenerating forest (Marsden *et al.* 1999). Principal component analysis (PCA) was performed to investigate if closely related variables could be combined to form a smaller number of composite and unrelated variables. Differences between habitat variables were analysed using unpaired t-tests and Mann-Whitney U tests.

3. Results

3. 1. Habitat

A total of 115 census points were sampled (Primary = 47, Secondary = 68). Mean habitat variables were calculated and analysed for each site and both habitats (Table 2). There were no significant differences between the two secondary forest sites as values for habitat variables were similar. However, between the two forest types there were some clear differences. Firstly, there was a clear decrease in tree height with regards to increased habitat disturbance; unpaired t tests showed differences between forest types to be highly significant with primary forest considerably higher. Secondly, tree density in secondary forest was markedly greater and increased in sites with high levels of disturbance (Table 2). Although the proportions of tree architectures was similar between the two secondary sites, Mann-Whitney *U* tests show there was a marginally significant difference between the forest types.

Table 2: Mean habitat variables and analysis for both forest types (dashes signify no values).

	Height (m) ± SD	**DBH (m) ± SD**	**Elevation (m) ± SD**	**Tree Density (ha)**	**Fruit/Flower (%)**	**Arch[a] (%)**
Site 1	12.04 ±1.99	0.36 ± 0.22	161.34 ± 41.00	347.7	37.9	63
Site 2	15.90 ± 4.49	0.34 ± 0.17	152.21 ± 32.84	335.3	42.7	57
test (p)	-2.29 (0.08)[b]	0.25 (0.81)[b]	-0.68 (0.55)[b]	1.15 (0.33)[b]	-0.40 (0.34)[c]	-0.71 (0.23)[c]
Secondary[d]	13.09 ± 3.37	0.34 ± 0.04	153.4 ± 19.80	341.5	40.3	60
Primary	19.38 ± 6.99	0.28 ± 0.18	-	230.3	-	13
test (p)	-5.66 (0.01)[b]	0.21 (0.85)[b]	-	11.94 (0.00)[b]	-	1.74 (0.04)[c]

[a] Architecture: percentage branching below half the trees height.
[b] Unpaired t-tests.
[c] Mann-Whitney *U* tests.
[d] Mean habitat variables for site 1 and site 2.

Figure 4: Score plot of PCA1 and PCA2.

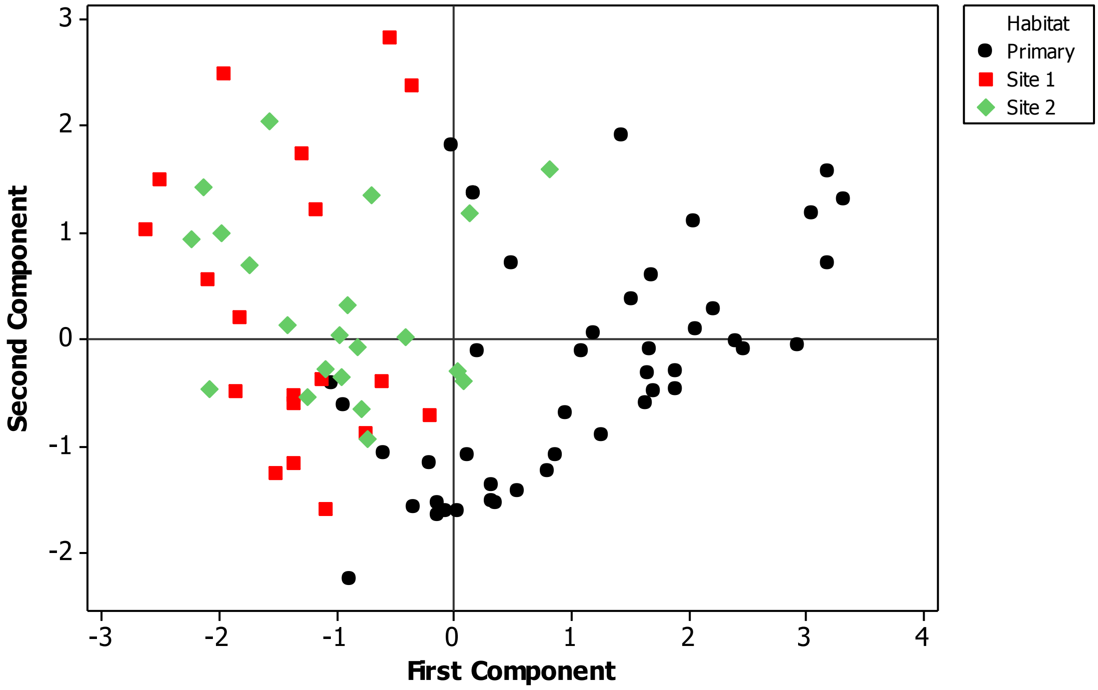


Table 3: Results of principal component analysis for habitat variables.

	PCA1	PCA2
Eigen Value	2.2281	1.2758
Cumulative percentage	44.6	70.1
Mean DBH[a]	0.344	<u>0.568</u>[b]
Mean Height	<u>0.596</u>	0.004
Architecture	-0.400	<u>0.471</u>
Mean Canopy Cover	0.296	<u>-0.597</u>
Mean Average Distance[c]	<u>0.528</u>	0.316

[a] DBH – Diameter at breast height

[b] Values underlined denote relationships.

[c] Average distance to the sampled trees at each point.

Principal component analysis (PCA) was used to compress the set of variables into a smaller axis of habitat variability. There were strong correlations between the habitat variables recorded. PCA extracted two factors with eigen values >1.0 which together accounted for 70.1% of the variability in the five original variables (Table 3). PCA 1 clearly shows an axis with a relationship between mean tree height and distance to survey tree (i.e. tree density). Plots that scored high in this factor have tall trees and are less dense which is characteristic of primary forest, whereas plots with low scores are the opposite and can be classed as secondary forest. This is supported by plots of PCA 1 and PCA 2 which clearly show separation of both habitats (Figure 4). PCA 2 accounted for less variation than PCA 1 (25.5%) and there is overlapping of the two habitat types. Figure 4 shows apparent overlapping of both secondary sites which, taken together with the results from table 3, suggests that these to forest types can be combined for further analysis.

Table 4: Summary of population density estimates (individuals / km^2) in secondary and primary sites split by species group. All densities derived from DISTANCE.

	Primary ± SE	**Secondary ± SE**	**Z test (p value)**
Parakeets	77.87 ± 22.29	141.44 ± 8.34	-2.67 (0.008)
Parrots	35.80 ± 5.88	30.87 ± 4.59	0.661 (0.509)
Macaws	21.20 ± 7.15	53.76 ± 11.97	-2.335 (0.019)
Other*	30.76 ± 7.09	22.385 ± 7.80	0.794 (0.427)

*Other accounts for none *psittacine* species e.g. Spix's Guan *Penelope jacquacu* and White Throated Toucans *Ramphastos tucanus*.

3.2 Parrot Group Size and Abundance

In total there were 131 km of census walks, 54 km in primary forest and 77 km in secondary with 585 sightings. All but one of the 15 parrot species previously observed in the area were recorded during the fieldwork; the exception was *Ara manilata* (Table 5). The number of groups and individuals encountered per kilometre was greater in secondary forest with *B. cyanoptera* the most commonly encountered. In secondary forest, thirteen parrot species were recorded with the exception of *A. ararauna.* All four species of parakeets (66% of sightings, n = 254), *A. severa* (17% of sightings, n = 48) and *A. farinosa* (5% of sightings, n = 20) were encountered regularly during surveys with the remaining species only occasionally observed. *Ara ochrocephla* was recorded once in secondary forest and not at all in primary. Twelve species were observed in primary forest; the two missing were *P. couloni* and *A. ochrocephala.* The four species that dominated the encounters and accounted for 58%

Table 5: Summary of parrot group size and abundance for individual species split between forest types (dashes signify no observations).

Species	**N Groups**		**Mean Group Size ± SD**		**Groups/km²**		**Individuals (km²)**[a]		**Density/km² ± SD**[b]		**Z test (P)**
	P[c]	S[d]	P	S	P	S	P	S	P	S	
Scarlet macaw *Ara macao*	14	8	2.71 ± 1.77	2.25 ± 0.46	0.26	0.10	0.70	0.23	22.81 ± 7.62	6.92 ± 1.09	2.07(0.03)
Blue and yellow macaw *Ara ararauna*	3	-	2.00 ± 0.00	-	0.06	-	0.11	-	-	-	-
Red and green macaw *Ara chloroptera*	5	5	1.80 ± 0.45	2.60 ± 0.55	0.09	0.06	0.17	0.17	-	-	-
Chestnut-fronted macaw *Ara severa*	8	48	3.00 ± 0.93	2.88 ± 1.18	0.15	0.62	0.44	1.79	42.84 ± 5.29	34.98 ± 4.60	0.30(0.77)
Blue-headed macaw *Primolius couloni*	-	3	-	1.67 ± 0.58	-	0.04	-	0.06	-	-	-
Mealy parrot *Amazona farinosa*	44	20	3.68 ± 1.83	4.45 ± 1.61	0.81	0.26	3.00	1.16	22.03 ± 4.41	19.63 ± 5.90	0.06(0.95)
Yellow-crowned parrot *Amazona ochrocephala*	-	1	-	4.00 ± 0.00	-	0.01	-	0.05	-	-	-
Blue-headed parrot *Pionus menstruus*	22	3	2.77 ± 2.76	3.42 ± 1.10	0.41	0.34	1.13	1.16	11.24 ± 2.49	27.57 ± 9.15	-1.51(0.13)
White-bellied parrot *Pionites leucogastor*	10	4	3.70 ± 1.64	1.68 ± 3.37	0.19	0.05	0.85	0.26	-	-	-
Orange-cheeked parrot *Pionopsitta barrabandi*	4	7	3.25 ± 1.71	4.14 ± 1.35	0.07	0.09	0.24	0.47	-	-	-
White-eyed parakeet *Aratinga leucophthalmus*	5	30	5.00 ± 2.35	5.83 ± 2.81	0.09	0.39	0.49	2.27	9.87 ± 4.04	102.41 ± 30.98	-2.96(0.003)
Black-capped parakeet *Pyrrhura rupicola*	20	59	5.00 ± 3.20	6.97 ± 4.12	0.37	0.77	1.85	5.34	29.16 ± 8.51	100.11 ± 15.36	-4.04(<0.001)
Cobalt-winged parakeet *Brotogeris cyanoptera*	30	121	9.06 ± 4.39	7.93 ± 4.33	0.56	1.57	5.02	12.47	75.14 ± 17.14	189.13 ± 20.57	-4.26(<0.001)
Dusky-headed parakeet *Aratinga weddellii*	3	44	7.00 ± 3.46	6.18 ± 4.31	0.06	0.57	0.39	3.53	27.35 ± 14.93	102.81 ± 21.62	-2.87(0.004)
Other[e]	35	4	2.39 ± 1.40	2.75 ± 0.96	0.65	0.05	1.59	0.14	-	-	-

[a] Number of individuals encountered per kilometre.
[b] Density estimates derived from DISTANCE. Only species with counts greater than 20 were included for individual analysis.
[c] Primary forest.
[d] Secondary forest.
[e] All non-psittacine species encountered.

of observations in primary forest were *A. farinosa* (22%, n = 44), *P. menstruus* (11%, n = 22), *P. rupicola* (10%, n = 20) and *B. cyanoptera* (15%, n = 30). Encounter rates were generally higher in secondary forest but it should also be noted that encounter rates for large macaws was greater in primary forest.

Parakeets were the most abundant group in both forest types but had a significantly higher population in secondary forest (Z =- -2.67, p = 0.008) (Table 4). Macaws were also significantly more abundant in secondary forest (Z = -2.67, p = 0.019), although the majority of encounters were smaller bodied macaws e.g. *A. severa*. In all the species for which density estimates were possible (Table 5), all four parakeet species had significantly higher density estimates in secondary forest especially for *B. cyanoptera* which had a density estimate greater than 180 individuals per km^2. The only species that had a significantly higher density in primary forest was *Ara macao*.

In secondary forest, average detection distance was 23.8 m with the greatest number of detections occurring less than 60 m (n=338) from the observer. Detections clearly decrease as distance increases. In primary forest detection distances averaged at 36.1 m ranging from 0 m to 150 m with the majority of detections occurring between 0 m to 40 m (n=178). Distances over 150 m were minimal so the data set was truncated to 150 m to help improve the fit of the detection functions (Buckland *et al.* 2001).

3.3 Foraging ecology and diet

A total of 213 foraging events (116 from foraging walks and 97 opportunistic events) were recorded involving 12 of the known psittacines in the area (Table 6). The species not encountered foraging were *P. couloni*, *A. ochrocephala* and *A. manilata.* A number of non-psittacines were also noted as they were observed competing for food resources e.g. Spix's guan *Penelope jacquacu* and Emerald toucanets *Aulacorhynchus prasinus* (referred to as 'Other'). *Pionus menstruus*, *P. leucogastor* and *P. barrabandi*, now referred to as 'mixed parrots', have been combined for all further analysis due to their low individual counts. Overall, the three most commonly encountered species were *B. cyanoptera* (20.7%, n = 44), *P. rupicola* (16.4%, 35), and *A. severa* (15.5%, n = 33).

Table 6: Foraging events, mean group size, plant part eaten and chi-squared expected results for psittacine species (dashes signify no observations).

					Food Type (%)[a]			
Species		**N (Exp)**	**# Ind**	**Mean Group Size ± SD**	**F**	**Fl**	**S**	**P**
A. ararauna	P[b]	9 (2.96)	28	3.11 ± 2.26	-	56	11	33
	S[c]	0 (6.04)	-	-	-	-	-	-
A. macao	P	15 (6.57)	44	2.93 ± 2.22	-	20	20	60
	S	5 (13.43)	16	3.20 ± 1.09	-	60	20	20
A. chloroptera	P	3 (0.99)	8	2.67 ± 1.53	-	-	-	100
	S	0 (2.01)	-	-	-	-	-	-
A. severa	P	2 (10.85)	9	4.50 ± 0.71	-	50	-	50
	S	31 (22.15)	111	3.58 ± 1.91	-	77	19	4
A. leucophthalmus	P	4 (8.22)	26	6.50 ± 6.61	-	25	25	50
	S	21 (16.78)	136	6.48 ± 4.58	-	57	43	-
A. weddellii	P	1 (4.60)	8	8.00	-	100	-	-
	S	13 (9.40)	76	5.85 ± 4.96	-	69	32	-
P. rupicola	P	11 (11.50)	53	4.82 ± 2.44	9	9	27	45[d]
	S	24 (23.50)	113	4.71 ± 2.35	-	79	13	8
B. cyanoptera	P	1 (14.46)	36	36.00	-	100	-	-
	S	43 (29.54)	313	7.28 ± 6.15	-	76	19	5
Mixed parrots[e]	P	4 (2.63)	11	2.83± 0.764	-	-	50	50
	S	4 (5.37)	14	3.67 ± 1.15	-	50	50	-
A. farinosa	P	13 (4.60)	109	8.38 ± 9.62	38	8	23	31
	S	1 (9.40)	3	3.00	-	100	-	-
Other[f]	P	7 (2.63)	21	2.70 ± 0.99	55	-	-	45
	S	1 (5.37)	1	1.00	-	100	-	-

[a] Food types: F = Fruit, Fl = Flower, S = Seeds and P = Pulp.
[b] Primary
[c] Secondary
[d] Invertebrates 9%
[e] *Pionus menstruus, P. leucogastor, and P. barrabandi* were combined as observed counts were less than five.
[f] Other non-psittacine species.

The combined habitat types show the psittacine community foraged on 22 food plant species from 18 families and one case of termite foraging (Table 8). The three most extensively exploited tree species, which account for 72% of the overall number of events, were *Ochroma pyramidale* (52%, n = 111), *Euterpe precatoria* (12%, n = 26) and *Cecropia peltata* (8%, n = 17). Psittacines in this community ate a wide variety of plant parts including flowers (55%, n = 117), seeds (21.5%, n = 46), pulp (18%, n = 38) and fruit (5.5%, n = 12). All birds consumed unripe (n = 11) and ripe (n = 33) seeds and fruits.

Chi-square tests show there is a significant difference between the two habitats with regards to foraging events encountered (x^2 = 112.195; df = 10; p = <0.001). For this analysis a number of sample sizes were too small for a meaningful analysis e.g. mixed parrots, however, species such as *B. cyanoptera* and *A. severa* were actually observed underutilising resources in primary forest and over exploiting resources in primary forest (Table 6).

Primary forest **–** In this habitat 70 (33%) events were recorded involving 11 psittacine species. Three species were not encountered; these were *P. barrabandi*, *P. couloni* and A. *orhocephala*. The three most commonly encountered species, which accounted for 55.7% of all events were *A. macao* (21.4%, n = 15), *A. farinosa* (18.6%, n = 13) and *P. rupicola* (15.7%, n = 11). In primary forest, birds fed upon 18 food plant species from 15 families. There was more variety of food plant species with the majority of events recorded with *Euterpe precatoria* (30%, n = 21). The three bird groups were found to have a more generalised niche breadth (Table 7). Diet was comprised of all plant parts; pulp (45.7%, n = 32), flowers (20%, n = 14), seeds (20%, n = 14) and fruit (14.3%, n = 10). The only case of termite foraging was encountered in primary forest with *P. rupicola*.

Table 7: Levin's niche breadth for each psittacine group split between secondary and primary habitats.

	Secondary	**Primary**
Macaws	0.075 (n=127)	0.180 (n=89)
Parrots	0.276 (n=17)	0.127 (n=120)
Parakeets	0.047 (n=639)	0.291 (n=13)

Secondary Forest **–** In this habitat foraging events were commonly encountered with a total of 143 (67%) events observed. Only 10 psittacine species were observed foraging and there was a distinct lack of large bodied species with *A. ararauna*, *P. couloni* and *A. chloroptera* not encountered foraging. *Brotogeris cyanoptera* (30%, n = 43), *A. severa*

(21.7%, n = 31) and *P. rupicola* (16.8%, n = 24) accounted for the bulk of the foraging events. Psittacines were found to feed on 10 food plant species from 9 families, a decrease of 8 available species compared to primary forest. The two most exploited food plant resources were *Ochroma pyramidale* (76%, n = 109) and *Cecropia peltata* (11%, n = 16) with both these species accounting for 87% of events.

Table 8: Plant species, item eaten, foraging records with percentage of records according to total foraging events.

Plant Taxa	**Parrot species[a]**	**Plant part[b]**	**Total records (%)**	**Vegetation Type**
ANNONAREAE				
Oxandra polyantha	*P. rupicola* *Other[c]*	F	4 (2)	Primary
ARECACEAE				
Iriartea deltoidea	*A. ararauna* *P. rupicola* *A. farinosa*	Fl	3 (1)	Primary, Secondary
BOMBACACEAE				
Ochroma pyramidale	*A. ararauna* *A. macao* *A. severa* *P. barrabandi* *B. cyanoptera* *A. weddellii* *P. rupicola* *A. leucophthalmus* *Other*	S, Fl	111 (52)	Secondary
BROMELIACEAE				
Aechmea angustifolia	*P. rupicola*	S	2 (1)	Primary
CLUSIACEAE				
Symphonia globulifera	*A. macao* *A. ararauna* *A. severa* *P. menstruus* *A. farinosa* *P. leucogastor* *P. rupicola* *A. weddellii*	Fl	12 (6)	Primary, Secondary
FABACEAE				
Erythrina poeppigiana	*A. macao* *A. leucophthalmus*	Fl	2(1)	Primary, Secondary
Inga alba	*A. macao* *A. ararauna* *A. leucophthalmus* *P. rupicola*	P	5 (2)	Primary
Swartzia arboresens	*Other*	P	1 (0.5)	Primary
Tachigali vasquezi	*A. leucophthalmus*	P	1 (0.5)	Primary

Plant Taxa	**Parrot species**[a]	**Plant part**[b]	**Total records (%)**	**Vegetation Type**
ICACINACEAE				
Leretia cordata	*P. rupicola*	P	1 (0.5)	Primary
LECHTHIDACEAE				
Bertholletia excelsa	*A. macao* *A. ararauna*	S	2 (1)	Primary
MENISPERMACEAE				
Anomospermum boliviana	*P. menstruus*	P	1 (0.5)	Primary
MORACEAE				
Ficus spp.	*Other*	F	1 (0.5)	Primary
Pseudolmedia laevis	*A. farinosa*	F, P	4 (2)	Primary
PALMACEAE				
Euterpe precatoria	*A. ararauna* *A. macao* *A. chloroptera* *A. severa* *P. leucogastor* *A. farinosa* *A. leucophthalmus* *P. rupicola* *Other*	S, P, Fl	24 (12)	Primary, Secondary
RUBIACEDE				
Palicourea plowmanii	*Other*	F	1 (0.5)	Primary
RUTACEAE				
Zanthoxylum huberi	*A. leucophthalmus*	S	1 (0.5)	Secondary
Zanthoxylum tambopatense	*P. leucogaster* *P. menstruus* *P. rupicola* *B. cyanoptera*	S	4 (2)	Secondary
SAPATACEAE				
Pouteria trilocularis	*A. farinosa*	F, S	3 (1)	Primary
SOLANACEAE				
Solanum macranthum	*A. severa*	S, P	3 (1)	Secondary
URTICACEAE				
Cecropia peltata	*A. severa* *B. cyanoptera* *P. rupicola* *A. leucophthalmus* *A. weddellii*	S, Fl	16 (8)	Secondary
Other				
Unidentified	*A. severa* *A. macao*	P	10 (5)	Secondary
TERMITES	*P. rupicola*		1 (0.5)	

[a] See table 4 for full species names.
[b] Plant part eaten: Fl – flower, F – fruit, S – seeds and P – pulp.
[c] Other non-psittacine species.

This lack of variety with regards to food plant species available in secondary forest created a narrower niche breadth when compared to primary forest (Table 7). Parakeets were calculated to have the narrowest niche breadth and only fed upon 6 food plant species from 5 families. The opposite occurred in primary forest when parakeets were generalists when foraging, feeding upon 9 food plant species from 8 families. There were a number of similarities between the plant species that psittacines were observed foraging upon at each habitat, for example foraging events were observed on *Symphonia globulifera* and *Euterpe precatoria* at both of the habitat types (Table 8). Secondary forest diet mainly comprised of flowers (72.7%, n = 104), seeds (23%, n = 33) and pulp (4.3%, n = 6).

4. Discussion

4.1 Habitat Association

The results here reveal that at least part of the parrot community can thrive in a modified landscape. In secondary forest there were only two species that were not encountered; A. *manilata* and *A. arauana*. Both were expected, the former because it is known to inhabit swamp areas (Bonadie 2000), and the latter because it is known to be uncommon. Although there are no previous parrot counts documenting the differences between forest types in the area, the overall number of individuals / km^2 in secondary forest is in some cases higher than in primary forest.

The sites sampled in this study both contained secondary rainforest which varied in both habitat quality and degree of human activity: site one contained secondary forest which was surrounded by relatively pristine forest, site two was more degraded and had higher levels of human activity. Although the two sites differed in location, habitat analysis suggested that there was little overall difference between variables. As expected the results from the study show that there are clear differences between habitats especially with regards to tree height and tree density. As a result of these differences bird-habitat relationships are thought to be closely correlated with structural characteristics (Cody 1981) or plant species composition of the habitat (Wiens 1981).

The fact that species richness / abundance were highest in secondary forest was somewhat unusual (see Lloyd (2004)). The bulk of the population in this forest type consisted mainly of the four parakeet species and *A. severa*. Encounters of these smaller bodied species were common suggesting a positive association with secondary forest. On the other hand, encounters of larger bodied species were perhaps because macaws are known to decline with increases in human activity (Karubian 2005). Lloyd (2004) also found similar observations with regards to the three large macaw species (*Ara araruana*, *Ara chloroptera* and *Ara macao*) which occurred at higher densities in primary forest and were rarely encountered in disturbed forest

It is not known why there was a higher proportion of parakeets but other studies have suggested that after a landscape has been modified, smaller bodied parrots frequently increase in abundance as the larger species decline presumably due to change in resource availability (Karubian 2005). Thus, these anthropogenic changes can drastically reduce the ratio of large to small parrots in a community. Furthermore, this change in ratio may also hamper future plant reproduction and regeneration in modified landscapes as removing large bodied seed predators will increase floral predators and potential dispersers of small seeds (Matuzak *et al.* 2008). The proximity of intact forest to the secondary sites (e.g. site 1) may also be important, not just by boosting overall richness and abundance, but by also influencing community composition. Adjacent primary forest may allow a wider variety of resources to be available which would not be found in modified forest and provide an alternative supply of these important resources at critical times of the year (Renton 2002).

4.2 Foraging ecology and diet

Most of the differentiation in bird abundance between the forest types could be attributed to differences in resource availability. This study was successful in identifying keystone resources which may drive diversity and abundance. When in secondary forest the psittacine community exhibited a specialised diet primarily exploiting the flowers and seeds from both *Ochroma pyramidale* and *Cecropia peltata*. The former was the most commonly exploited resource and was foraged upon by seven psittacine species. These pioneer trees are known food sources for *Pyrrhura* and *Brotogeris* in the Atlantic forest, Brazil (Marsden *et al.* 2000), also for *A. severa* populations in Manu, Peru (Gilardi 1996) and in Costa Rica at least for *A. macao* (Vaughan 2006). With regards to *Cecropia peltata*, Marsden *et al.* (2000) found Blue-chested parakeets *Pyrrhura cruentata* to be strongly associated with altered habitat due to the high proportions of the pioneer tree species Cecropiaceae in their diet, this study also shows this as an important food source to many parakeet species.

Ochroma pyramidale and *Cecropia peltata* flowers comprised the most common food item (72.7% of secondary forest observations) and were observed to be the largest proportion of food items found for all parakeet species and *A. severa*. Foraging on flowers may confirm the general characterisation of psittacines as potential pollinators. Pollination is important for plant survival and has only recently been recorded in the Amazon: Cotton (2001) reported the pollination of *Platonia insignis* (Clusiaceace) by both White-eyed parakeets *A. leucophthalmus* and White-bellied parrots *P. leucogaster*. The extensive foraging of psittacines on the flowers of *Ochroma pyramidale* and *Cecropia peltata* may explain their abundance in secondary forest. However, it is unclear if the birds heavily foraged on these resources due to their abundance, quality or both. Therefore, it would be interesting to analyze in future studies the nutrient content and whether psittacines may function as pollinators since this has been recorded in other tree species (Galetti 1993; Cotton 2001; Ragusa-Netto 2004; Ragusa-Netto 2006).

In contrast to secondary forest, psittacines were observed feeding on a wider range of resources in primary forest, thus exhibiting a more generalised diet. The presence of a greater number of food plant species (18 species from 15 families) may explain the greater number of foraging events with regards to parrots and macaws. It seems that larger bodied species are able to include a wider diversity of plant parts in their diets allowing them to forage on a variety of different resources (Galetti 1993). This is supported by the large proportion of fruit and pulp recorded in this forest type (60% of primary forest observations). In this habitat one case of termite foraging was also observed; foraging on termites is uncommon in Neotropical parrots and insects are thought to provide additional protein and fat in the diet (Renton 2006). Cases of insectivorous psittacines have been documented for their counterparts, the endemic Western Corella *Cacatua pastinator* in Australia (Smith 1991).

4.4 Seasonality

Tropical frugivorous birds are known to have large seasonal population fluctuations following changes in food resources (Loiselle *et al.* 1993), rainfall (Poulin *et al.* 1993) and breeding season (Poulin *et al.* 1993). Hence they exhibit movements within habitat mosaics in a daily, monthly and seasonal basis causing their presence at a given habitat not to be uniform (Gilardi *et al.* 1998). The observed levels of psittacine populations in secondary forest may have been a temporary effect and due to the observed levels of foraging activity in primary forest, this forest type may be important all year round. The study time period may have overlapped with a period of low or high psittacine abundance, leading to exaggerated estimates resulting in inaccurate measures of population abundances (Terborgh *et al.* 1990). Hence, surveys need to be conducted throughout the year or in different seasons in order to account for potential seasonal variation in abundance. It has also been estimated that a sampling effort of hundreds of kilometres is required in order to produce reliable estimates (Thoisy *et al.* 2008) which is considerably more than the effort produced for this study.

As well as playing a role in abundance, seasonality also plays an active role in food availability. Diets of parrots have been found to vary seasonally in Australia (Long 1985) and elsewhere in the Neotropics (Renton 2001). Renton (2001) observed psittacines in western

Mexico exhibiting a narrower niche-breadth in the dry season compared to the wet season in response to low food availability. The results here partially support the hypothesis that movements are influenced by temporal changes in local food availability. Renton (2002) also found that similar species of macaws were less abundant during the dry season in eastern Peru and suggested that this may be related to food availability. The low number of large macaws encountered foraging in secondary forest may also coincide with a sharp decline in plant energy production in the forest during the dry season months of May to August (Renton 2002). Such results suggest that psittacines track changes in food availability and the presence of food plant species in secondary forest is undoubtedly important.

4.5 Conclusion

As more areas in the Neotropics are converted to different land uses and becoming heterogeneous, the persistence of parrots may be linked to exploiting tree species in secondary habitat. Conservationists and land managers are increasingly seeing the benefit of habitat mosaics in conservation efforts to preserve wildlife (Marsden *et al.* 2008) and it may actually be more effective to incorporate anthropogenic habitats into reserves rather than just preserving pristine forest (Law *et al.* 1998).

The main limitation encountered was the time constraints, as a longer study would have provided more habitat variables to be recorded and better data with regards to population estimates. Regardless of the short term nature of this study it is unquestionable that pristine forest is important for psittacine communities; results from this study also highlight the importance of secondary forest. In light of the findings in this study, I believe that secondary forest has a special habitat value not just for this parrot community but potentially for all communities in the Neotropics. However, without more information on diet and populations from a range of habitats the understanding of *psittacine* ecology will remain fragmented at best. Further in-depth studies which stretch throughout the year are vital in understanding the needs of *psittacines*. Only in this way will it be possible that the correct habitat elements are protected at the correct spatial scale.

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